

Convergent Evolution in the Dentitions of Grazing Macropodine Marsupials and the Grass-Eating Cercopithecine Primate *Theropithecus gelada*

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Abstract

This study examines the dentitions of two sets of non-ungulate grazers in relation to their diets. These sets were the grazing macropodine marsupials (including the genera *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes*) and the large, grass-eating cercopithecine primate *Theropithecus gelada*. The two sets are highly selective grazers whose diets consist mainly of green grass parts. Both were found to share four unusual dental adaptations for trituration of grasses and extension of the active life of the cheek teeth despite the severe abrasive effects of their diets: 1) bilophodont molars, which when worn present distinctive patterns of longitudinal and transverse enamel cutting ridges; 2) arrangement of the mandibular cheek teeth in an upwardly convex curve (reversed Curve of Spee) so that occlusion between these teeth and their maxillary counterparts is concentrated in a small anterior area of the tooth row instead of along its entire length; 3) accelerated antero-inferior movement of cheek teeth propelled by the anterior force of occlusion that permits relatively unworn, posterior elements of the cheek tooth battery to be moved anteriorly into areas of intensified function; and 4) enlargement of the transeptal interdental fibres of the periodontal ligament to maintain close contact between the elements of the cheek tooth row and thus convert the row into a single functional unit.

This convergent evolution of grazing macropodine marsupials and a grass-eating primate is particularly interesting because the adaptations for grazing are considered highly derived in both the macropodine and cercopithecine lineages, and that the pathway of evolutionary change followed similar courses in both groups. Adaptations for grass-eating are thought to have arisen in ancestral types of both lineages that subsisted on diets of softer, less resistant vegetation and that possessed dentitions that lacked specializations for the reduction of large quantities of abrasive, high-fibre vegetation and the preservation of relatively unworn tooth substance throughout adult life.

Introduction

Herbivores face considerable problems imposed by the high rate of wear on their teeth caused by mastication of large quantities of tough, fibrous and frequently abrasive vegetation. These problems are particularly serious in grazers, which consume large quantities of grasses that are rich in abrasives. Grasses contain endogenous abrasive silicates (phytoliths) that deter attack from herbivores, and potentially damaging exogenous abrasive materials such as sand and grit from soil. Many mammalian species have evolved various combinations of dental modifications to enlarge the surface area of the postcanine teeth, to prolong the life of these teeth, or both that compensate for the rapid rate of dental wear caused by these abrasive materials. Enlarging the total surface area of the cheek tooth permits better subdivision of plant material into small parts, although this requires increased muscular force. This increased subdivision facilitates either direct digestion of starch or indirect digestion of cellulose through microbial symbionts. A similar effect is gained by increasing the total length of the tooth's enamel cutting edges.

The strategies that have evolved in various mammalian lineages for the exploitation of grasses as a primary source of food are many and varied, with each grazing lineage possessing its own unique combination of features for harvesting, chewing and digesting grass parts. Because grass is low in simple sugars, low in protein and high in fibre, successful grazers must strike a balance between the metabolic energy they expend in processing grass and the energy they receive in return. The complex carbohydrates present in grasses cannot be directly metabolized by mammals, and so most grass-eating mammals have evolved modifications of their digestive tracts for fermentative breakdown of these carbohydrates into usable sugars and volatile (short-chain) fatty acids. The two basic styles of gut fermentation that have evolved in mammals, foregut fermentation and hindgut fermentation, differ in their efficiencies and have been incorporated in two rather divergent feeding strategies in the animals that use them. Foregut fermenters (e.g. artiodactyls, kangaroos, and colobine monkeys) extract high metabolic yields from moderate amounts of relatively high-quality forage, while hindgut fermenters (e.g. perissodactyls) rely on bulk feeding of lower-quality forage to compensate for a reduced nutrient extraction rate (Janis 1976). Accordingly,

the teeth of foregut fermenters tend to be somewhat simpler in design than those of hindgut fermenters because they are required to process less vegetation of generally higher quality (*i.e.* lower in fibre and abrasives, and higher in water content).

The mechanical properties of foods differ, with some requiring more compression or crushing and others (such as grasses) requiring more cutting or shearing. An optimal crush/shear ratio exists for breaking up each type of food (Osborn & Lumsden 1978), and the masticatory apparatus of every species has evolved, in part, to generate the crush/shear ratio best suited to its preferred diet. As discussed by Osborn (1993), this ratio depends on the direction of tooth movement during mastication, the orientation of the occlusal surfaces of the teeth and the direction of the bite force.

Feeding on grasses is usually related to the evolution of several specific dental modifications that are used in various combinations. The most common of these modifications include an extreme increase in the surface area of the teeth, the evolution of complex enamel patterns on the occlusal surfaces, an increase in the height of the crowns of the molars, and the conversion of the molars into rootless, continuously growing structures. Of these, the first two act more to increase the surface area and food-processing efficiency of the tooth while the last two act to prolong the life of the tooth. The high-crowned (hypsodont) molars of certain perissodactyls, artiodactyls and rodents, for example, are usually associated with an abrasive diet and are commonly assumed to have evolved in response to the consumption of abrasives associated with grasses (Stirton 1947; Janis & Fortelius 1988). Manatees (genus *Trichechus*), consumers of sea grasses, have evolved yet another strategy – that of continuous posterior eruption of an indefinite number of new molars in response to the wear and anterior shedding of the anterior molars (Domning & Hayek 1984).

Because the dentition is only one part of the grazer's digestive armament, it breaks down grasses in a manner that is complementary to the type of fermentation that will occur in the gut. On the basis of the rather limited number of major types of molar and jaw design we see in grazing mammals, however, there would appear to be design constraints that are operating on the evolution of these structures in specific lineages. Some of these constraints no doubt derive from the mechanical properties of the dental hard tissues themselves and the need to minimize the potential for crack propagation in brittle enamel (Koenigswald *et al.* 1987). In each grazing lineage, there is a unique compromise between the size of individual cheek teeth, the design of the occlusal surfaces of the teeth, the total number of cheek teeth an animal can develop in its life, and the number of teeth in occlusion at any one time. The anatomical compromise that evolves in any grazing lineage is teeth that must be powerful enough to physically break down grasses yet durable enough to last through the entirety of the animals' reproductive lives. Increasing the amount of tooth material (and therefore the area and total length of cutting edges) is one solution for increasing grass comminution and reducing wear. However, the cost of larger teeth to the animal, in the development of the teeth themselves, in larger masticatory muscles and in dental supporting tissues, is great. An enlarged masticatory apparatus is energetically costly to construct and maintain, and in some lineages the costs appear to outweigh the benefits.

Among mammals, neither herbivorous marsupials nor primates exhibit the extreme dental modifications for coping with high rates of dental wear seen in lineages with long evolutionary histories of grazing (*e.g.* perissodactyls or artiodactyls). Yet, among both the Metatheria and the Primates there are species that rely exclusively on diets of grasses. These species display unusual dental modifications that increase the efficiency of the postcanine teeth in the comminution of grasses and that prolong the life of the postcanine dental battery, but that differ from those of other more widely known grazers (Jablonski 1981). In this study, the dentitions of the grazing Australian macropodine marsupials comprising the genera *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes* and the large cercopithecine monkeys known as geladas or gelada baboons (*Theropithecus gelada*) of the highlands of central Ethiopia are examined. These groups have been compared because of the remarkable similarities observed in their postcanine dentitions. Similarities in diet and dental morphology between the grazing macropodines and the geladas are explored in detail. The evolutionary histories of these animals are then compared to see if the apparent convergence in dental structure and function between the groups can be related to similarities in selective pressures acting on similar ancestral morphologies in their respective lineages.

Dental Structure and Function in Relation to Diet

Grazing Macropodines

Among the extant Macropodidae, species of *Macropus*, *Peradorcas*, *Onychogalea* and *Lagorchestes* have been classified as grazers because of their reliance on abrasive, high-fibre vegetation often in the form of grasses. Although some species-specific and regional variations in dietary preferences have been reported among these species, grasses dominate their diets (Jarman 1984). For instance, the diet of *Macropus giganteus* in southwestern Queensland is supplemented by dicotyledons throughout the year (Griffiths & Barker 1966, Griffiths *et al.* 1974), while that of *M. rufus* includes drought-resistant shrubs in dry times (Jarman 1984). Grazing macropodines are highly selective feeders, which can use their narrow muzzles and incisal arcades to pick individual grass blades. They show a preference for green, readily digestible material and avoid, where possible, highly fibrous and dry plant parts (Jarman 1984).

The structure and function of the teeth in grazing macropodines was described in detail by Sanson (1978, 1980), who defined a series of five characters associated with a diet of abrasive, high-fibre plants. These were: 1) bilophodont molars with strong links (longitudinal ridges) between the transverse loph(id)s; 2) a convexly curved lower tooth row (describing a reversed Curve of Spee) that meets the upper row at a tangent so that only the anterior portions of the tooth row are in occlusion; 3) occlusion that consists of an initial forward motion of the lower molars followed by a marked lateral movement in which the developed links are in contact with the opposing lophs; 4) molar progression, by which relatively unworn lower molars are advanced to anterior positions in the jaw while worn molars are shed anteriorly; and 5) reduced or vestigial permanent premolars.

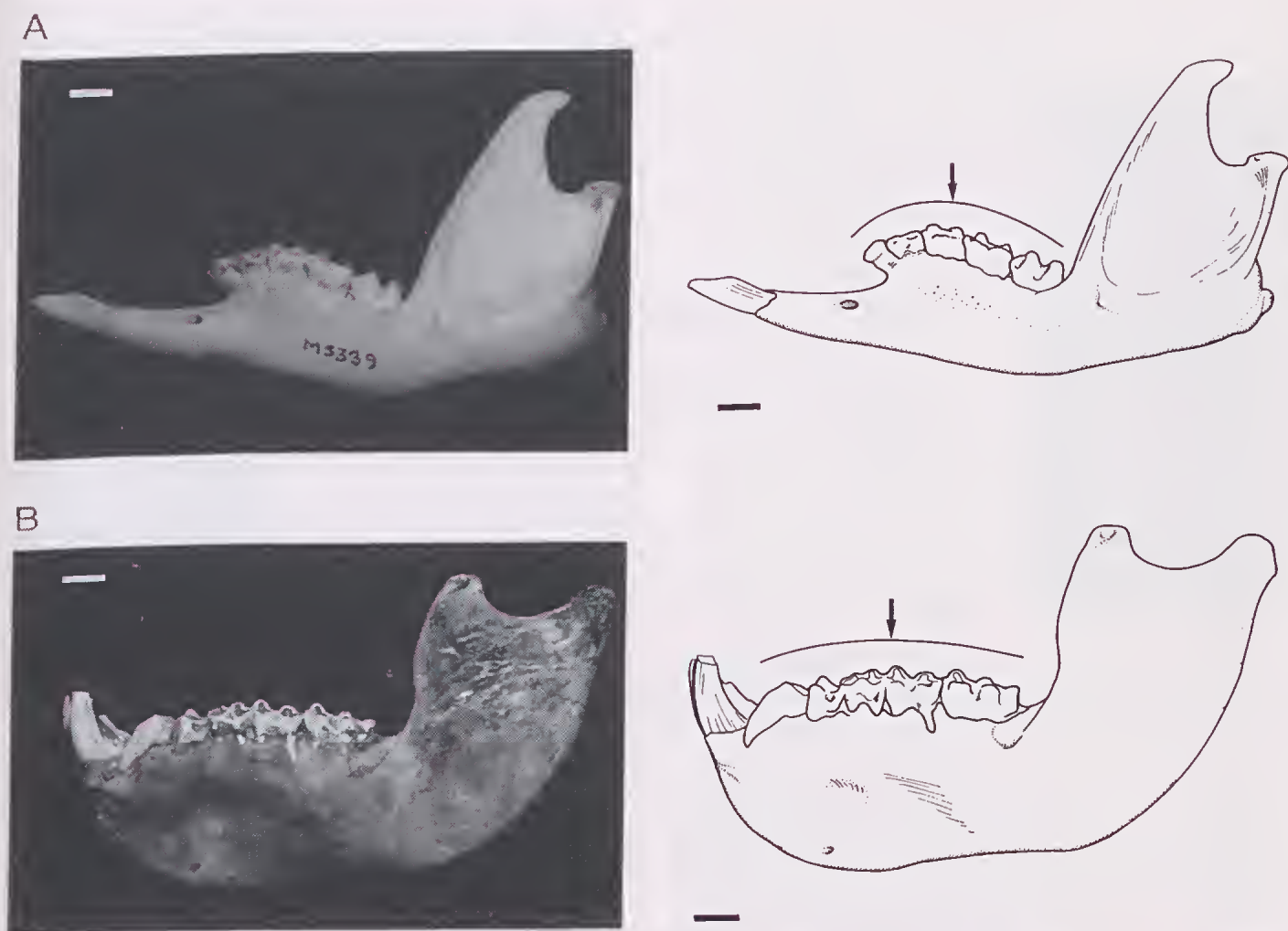


Figure 1. Comparison of the dentitions of a grazing macropodine (A; *Macropus robustus*; W.A. Museum M5339) and a grass-eating primate (B; *Theropithecus gelada* HKU/UWA 0242) in lateral view. In the line drawings of the same specimens, the curves represent the reversed Curves of Spee and the arrows indicate the regions of the dentitions at the most superior points on the curves where the forces of mastication are most strongly concentrated. Scale bars in all views indicate one centimeter.

These basic anatomical characteristics of the dentition of grazing macropodines are illustrated in Fig 1A and Fig 2A. The Curve of Spee is a term used to describe the upwardly concave profile of the human mandibular dentition as viewed from the side. A reversed Curve of Spee is an upwardly convex curve of the lower dentition.

As described by Sanson (1980), mastication in grazing macropodines is ideally suited to the comminution of tough, fibrous materials. Processing of plant materials is accomplished mostly by cutting on the sharp enamel edges of the molar teeth. Although the sharpest cutting edges are on unworn molars, further cutting edges are exposed as the enamel on the surface of the crown wears and the underlying dentine is exposed and excavated (Fig 2A). The efficiency of the molar increases up to a certain point, after which the molar is so worn that it is no longer effective as a cutting tool. Because the focus of cutting action is at the point of contact between two enamel cutting surfaces, the wearing down of those surfaces will result in diffusion of occlusal pressure over a larger area and less effective comminution (Sanson 1980).

As their functional life approaches an end, molars move into nonfunctional positions in the anterior portion of the

jaws before being shed. Through the process of molar progression, a molar tooth erupting in the mandible moves anteriorly and dorsally into the occlusal plane. The molar continues to move anteriorly and dorsally as it becomes worn and, at the height of its functional life, occupies a position on the most superior point on the reversed Curve of Spee (Figure 1). As the tooth wears further, molar progression moves it anteriorly and ventrally out of the occlusal plane until it is shed (Sanson 1980). This process begins with shedding of the premolars and their position in the jaw being taken by the first molar, with the other erupted molars following. Molar progression continues with the wearing down and shedding of the first, second and subsequent molars in succession (Tyndale-Biscoe 1973). The process of molar progression appears to be driven by the direction of the force of occlusion. Anteriad movement of the mandibular dentition relative to the maxillary dentition during mastication produces anteriorly directed forces that, in turn, are transmitted to the dentition as a whole by the transeptal interdental fibres of the periodontal ligament (Sanson & Miller 1979). These fibres act as links in a chain to maintain tooth-to-tooth contact. Normally, in kangaroos, only four molars erupt in each jaw so that very old individuals may have only one worn molar tooth left in each jaw. Thus, the

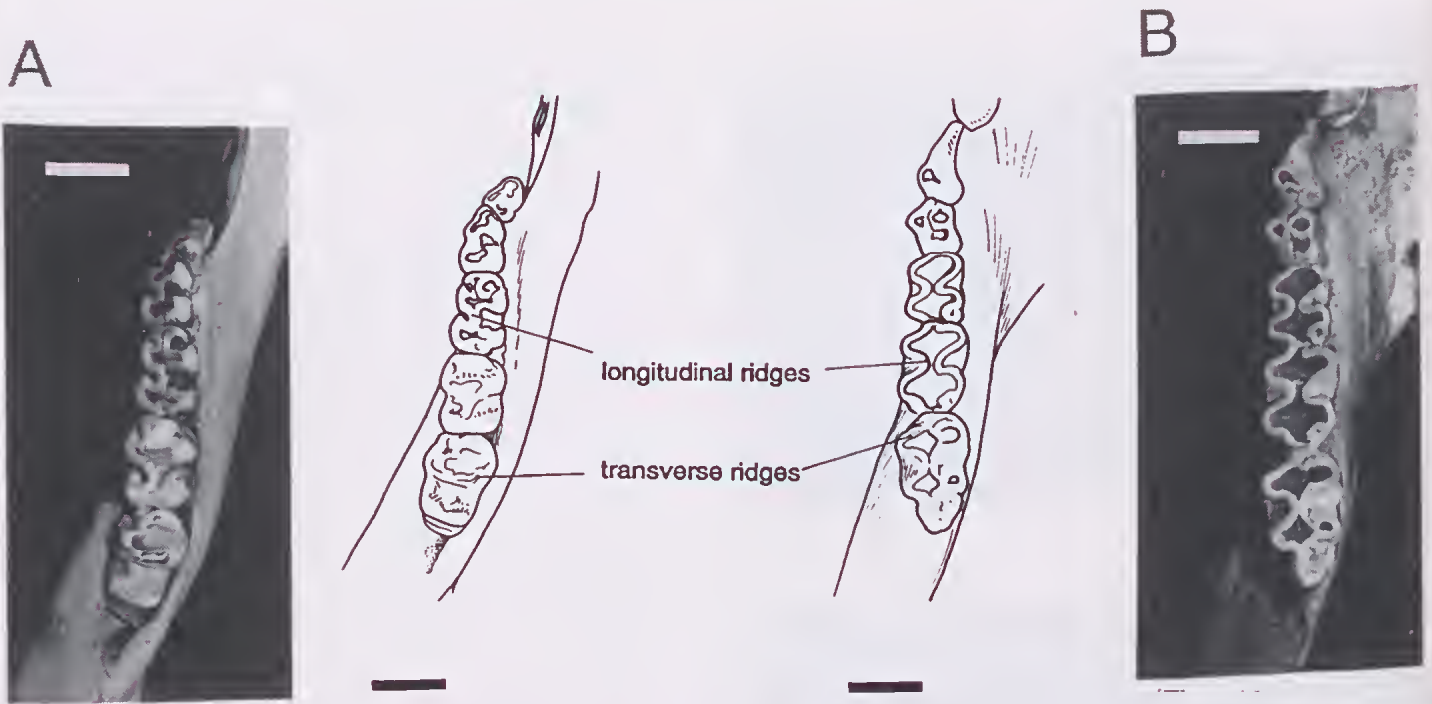


Figure 2. Cheek teeth of a grazing macropodine (*Macropus robustus*) and a grass-eating primate (*Theropithecus gelada*) in occlusal view (specimens as in Fig 1). Line drawings of the same specimen indicate the transverse and longitudinal enamel ridges that shear against their counterparts in the upper dentition to comminute grass parts during mastication. Scale bars in all views indicate one centimeter.

life span of these animals is dictated in large part by the durability of their teeth. Only in the little rock wallaby, *Peradorcas concinna*, are new molars continuously produced in the back of the jaws, apparently in response to a diet of grasses and ferns that are rich in abrasive silica (Sanson *et al.* 1985).

Theropithecus gelada

Among Primates, *Theropithecus gelada* is unique in its almost exclusive reliance on a diet of grasses. Geladas prefer grass blades to herbs or shrub vegetation when the former is available (see Iwamoto 1993a for a review). In the localities where the feeding behaviour of geladas has been observed throughout the year, grasses were found to constitute 90% of the diet in the wet season, but around 60% at the height of the dry season. Although green grass blades constitute most of the grass parts eaten, grass seeds are intensively exploited by geladas when they are available. Geladas are highly selective feeders but, unlike grazing macropodines which crop grass with their incisors, they harvest young grass blades between the highly opposable first and second digits of the manus before transferring them to the mouth. The same technique is used for the harvesting of rhizomes, which form an important part of the diet in the dry season (Iwamoto 1993a). Because geladas do not clean the rhizomes before ingestion, this increases their consumption of exogenous abrasives from the soil. Feeding is generally a continuous operation in which the animal masticates the previous handful of grass parts while gathering the next (Dunbar 1977). The time geladas spend feeding each day is longer in the dry season than in the wet season because the animals must spend longer to find green blades and succulent stem bases of grasses (Iwamoto 1993a, b). The ability of geladas to harvest vegetation quickly and with great precision appears to have been an ancient attribute of the *Theropithecus* lineage,

as judged by the fact that the digital proportions of the gelada were presaged in a Pliocene member of the lineage (Jablonski 1986).

In *T. gelada*, the demands of mastication of an abrasive, high-fibre diet are met with a series of structural modifications of the teeth and jaws that make possible particularly efficient trituration of large quantities of grass parts (Jolly 1972, Jablonski 1981, 1993a). In the dentition, these modifications comprise five major features: 1) bilophodont molars with columnar cusps that, when worn, present a pattern of complexly curved enamel cutting ridges; 2) alignment of the mandibular cheek teeth in a reversed Curve of Spee so that, for much of the life of the individual, contact between the upper and lower tooth cheek tooth rows is concentrated anteriorly; 3) occlusion that is characterized by a short antero-lateral movement followed by a marked lateral component that permits the transversely and longitudinally oriented enamel cutting edges in the lower cheek tooth row to move across those of the upper row; 4) accelerated mesial drift of the molar teeth promoted by heavy interproximal wear and delayed eruption of the lower third molars, by which relatively unworn molars are moved to more functional, anterior positions in the jaws; and 5) possession of enlarged mesial shelves and distal accessory cusps on the first and second permanent molars, and a large and consistently well-formed hypoconulid on the lower third molars in order to increase the functional length of the cheek tooth rows (Jolly 1972; Jablonski 1981, 1993a; Swindler & Beynon 1993). The basic anatomical characteristics of the dentition of *T. gelada* are illustrated in Fig 1B and Fig 2B.

The molars of the gelada display considerably more occlusal relief at most wear stages than do those of any other cercopithecines, but they probably approach optimum operational efficiency in a relatively unworn state when the

greatest number of exposed enamel ridges is available for separation of plant material (Jablonski 1981; Meikle 1977). In unworn molar teeth, the cusp pairs of the mesial and distal loph(id)s are partly separated by deeply waisted buccal and lingual enamel folds. When worn, this arrangement produces a series of incomplete transverse ridges of harder enamel alternating with softer dentine (Fig 2B). Because of the height of the cusps of the molars and the depth of the clefts and basins, the molars of *T. gelada* retain occlusal features for a long time (Meikle 1977). Further, the long buccal surfaces of the molar teeth permit the long anatomical crown to function until the root supporting system of the teeth is compromised (Swindler & Beynon 1993).

In *T. gelada*, the highest occlusal pressures can be generated at an anterior position in the jaws, at the apex of the reversed Curve of Spee (Jablonski 1981; see Fig 1B). During the early part of adult life, this is where the upper and lower first permanent molars come into contact, but as these molars wear and move anteriorly in the jaws their positions are gradually occupied by the anterior loph(id)s of the second permanent molars, followed by the posterior loph(id)s. The curved orientation of the lower tooth row, the action of mesial drift and the delayed eruption of the elongated lower third molar tooth help to ensure that relatively unworn tooth substance is retained until late in life (Jablonski 1981). In one mandibular specimen (HKU/UWA 0242), the fourth premolar showed severe wear of the interproximal enamel and a worn occlusal surface, the first molar was heavily worn on the occlusal surface while the second molar was only slightly so, and the large third molar was barely worn and the root apices were still open (Miller & Jablonski, unpublished observations). One of the effects of this process is the production of a steep wear gradient in the molars of *T. gelada*, characterized by considerably heavier wear in the anterior than the posterior molars at any given time (Jablonski 1981).

The mesial drift that occurs in the gelada is not the same as the molar progression in the grazing macropodines, in which the continual movement of molars is accommodated by sequential loss of anterior teeth. In *T. gelada*, all the molars are, generally, retained throughout life and are not shed, despite very heavy occlusal and interproximal wear. Near loss of anterior cheek teeth by shedding has only been observed in one aged female specimen, which interestingly, also possessed supernumerary upper fourth molars. In *T. gelada*, several features of the alveolar bone and periodontal ligament indicate that the cheek teeth are functioning and moving as a unit. These include the presence of buttressing bone around the mandibular cheek teeth and enlargement of the trans-septal interdental fibres of the periodontal ligament (Miller & Jablonski, unpublished observations). Anterior movement of the cheek teeth in the gelada appears to be driven, at least in part, by the anterior force of occlusion, but marked anterior movement (and shedding of obsolescent teeth anteriorly) seems to be prevented by the stabilizing effect of the large upper canine and lower sectorial premolar (Miller & Jablonski, unpublished observations).

Evolution of Dental Form and Function

The similarities in dental morphology shared between grazing macropodines and geladas are striking, despite major differences between the two groups in overall cranial

shape. Both groups possess bilophodont molars which, while different in the cusp and crest disposition in the unworn state, appear remarkably similar when moderately worn. The sequence of dentine and enamel ridge exposures produced by interproximal (interdental) wear and wear on the occlusal surfaces is virtually identical in both groups, although it appears that the more bunodont macropodine molars approach functional obsolescence earlier than those of the gelada.

The similarities between the groups in the conformation and movement of the cheek teeth in the jaws are perhaps even more remarkable than those of the teeth themselves, and distinguish them from their respective non-grazing relatives. In both groups, the reversed Curve of Spee acts to concentrate the muscular force exerted by the muscles of mastication in a relatively small, anteriorly located area of the tooth row. Molar progression in the macropodines and mesial drift in the geladas provide mechanisms by which animals of both groups are provided with a continuous supply of relatively unworn and highly efficient triturating surfaces to this focal point of occlusal pressure. The geladas' adaptation is the more conservative because heavily worn molars are retained in the jaws, resulting in an eventual flattening of the occlusal profile in old age and apparent dispersion of the force produced by the muscles of mastication over a larger area of the molar row. Anterior movement of molars continues throughout life in the gelada, but the continuous, slot-machine-like replacement of molars at the back of the jaws does not occur as it does in grazing macropodines or, as it does in the even more extreme form, in the manatee and *Peradorcas*. In this regard the geladas can be viewed as lying at the conservative end of a spectrum of dental and gnathic adaptations common in non-ungulate grazing mammals to extend the active life of the cheek teeth despite the severe abrasive effects of diet.

Discussion

Morphologists are quick to identify "adaptive features" in the animals they study, but it is difficult to prove or establish the adaptedness of these features without resorting to circular argumentation. Reference to conditions in an "outgroup" is a method that reduces circularity and, in the case of the animals under consideration here, the adaptedness of the dental morphology in one group is supported by that discovered in the other distantly related group. As Davis stated, "the convergent appearance of similar conditions in more or less remotely related organisms under similar or identical environmental conditions is the most readily available proof of adaptive value" (1949, p. 80).

The identification of a similar suite of dental characteristics in two phyletically distant lineages argues strongly in favour of the occurrence of convergent evolution of dental form and function in response to closely comparable environmental stimuli in the two lineages. Further, this demonstration of convergence argues strongly for the adaptive advantage of the unusual suite of features of the dentitions of the two lineages in relation to graminivory.

Sanson (1978) has argued that macropodines belonging to the "derived grazing grade" can be contrasted to those of the "ancestral browsing grade". Those macropodines he

assigned to the browsing grade (e.g. *Wallabia*, *Dorcopsis*, *Dendrolagus* and *Setonix*) subsist on diets of relatively non-abrasive vegetation of low fibre content, such as the leaves of dicotyledonous plants, and occasional fruit and flowers. Their dentitions lack the conspicuous adaptations for the processing of tough vegetation and the preservation of tooth substance, and instead are characterized by bilophodont molars with weak longitudinal ridges, a flat cheek tooth row in which the permanent premolar and the four molars in the upper and lower jaws meet each other along a flat occlusal plane, and modest amounts of mesial drift (Sanson 1978). The derived grazing grade of macropodines evolved from the ancestral browsing grade, Sanson (1978) reasoned, as a response to climatic and ecological events beginning in the terminal Miocene that spurred the decline of mesic vegetation in the central regions of Australia and the rise of xeric grasslands.

The specialized nature of the dentition of *Theropithecus* has been recognized for many years and, as in the case of the grazing macropodine dentition, is a relatively recent innovation that can ultimately be traced to late Tertiary climatic and ecological change. Although some aspects of the emergence of the genus are still not fully understood (see Jablonski 1993b), the *Theropithecus* dentition clearly represents a highly derived condition for the tribe comprising the largest cercopithecines, the Papionini. The dentitions of other papionins such as macaques (*Macaca*) and common baboons (*Papio*) more closely resemble the primitive condition for the tribe in the absence of conspicuous adaptations for exclusive graminivory. Compared with the molars of *Theropithecus*, their molars possess more bunodont crowns with shallow notches and clefts and are arrayed in a flat tooth row. Moderate levels of molar wear in these animals result in the exposure of a simpler pattern of exposed enamel and dentine on the occlusal surfaces and the production of a more even wear gradient along the cheek tooth row.

The emergence and early diversification of *Theropithecus* in the Pliocene in East Africa was clearly linked to the evolution of a feeding apparatus specialized for the eating of grasses (Jablonski 1981, 1993a). This made possible the invasion of the more open, grassland environments that were evolving in East Africa in the late Miocene. The specializations for grazing in *Theropithecus* included those of the hand — that permitted early theropithecids to harvest the vegetation of the emergent grassland environments — and those of the masticatory apparatus (Jablonski 1986, 1993a). *Theropithecus* thus occupies a position in what could be called the derived grazing grade for primates.

The dental specializations in both the grazing macropodines and the geladas represent apparent compromises between the demands of diet and constraints of dental and gnathic design in the two lineages. In both, the total length of the enamel shearing crests and cutting edges of the molars has been increased relative to that seen in their browsing counterparts (Benefit & McCrossin 1990) and, at least in the case of the geladas, it can be argued that these features could not have been increased further within the constraints of a bilophodont tooth. In addition, both lineages — with their reversed Curves of Spee and mechanisms of molar progression or mesial drift — have evolved similar, simple mechanisms for conserving relatively unworn occlusal surfaces long into adult life while maximizing the occlu-

sal pressures that can be exerted between opposing molar teeth. The reversed Curve of Spee concentrates occlusal pressures in a small area of the cheek tooth row and thus helps the animals make the most of molars that, by the standards of grazing ungulates, are relatively simple. It would thus appear that the constellation of dental features shared by grazing macropodines and geladas constitutes an alternative "blueprint" for facing the adaptive challenges of graminivory. This suggestion is supported by the fact that the bilophodont lower molars of manatees, which are consumers of sea grasses, are also arranged in a reversed Curve of Spee and also are shed and replaced through molar progression.

The many parallels between the diets and dental anatomies of the grazing macropodines and the geladas still leave us with the question of why the dentitions of these distant lineages evolved in such remarkably similar fashions. Both groups represent ungulate-like grazers in non-ungulate orders and so have evolved their dental specializations in lineages that lack the more established, long-term anatomical commitments to grazing seen in perissodactyl and artiodactyl lineages. The basic pattern of bilophodonty seen in the molars of both groups under consideration is itself thought to be a modification that evolved to facilitate the processing of vegetation. Bilophodont molars were well established within the Macropodidae and Cercopithecidae by Middle Miocene times or, possibly, earlier (Benefit 1987; Hume *et al.* 1989) and thus must be considered as ancient elements of their anatomies. The fact that the evolution of grazing adaptations in the dentitions of both lineages took very similar courses would tend to suggest that the basic template of bilophodonty in both lineages was the product of a rigid developmental pattern that acted to limit or constrain architectural possibilities within the dentitions of both groups (Janis & Fortelius 1988). Such constraints may have seriously limited the potential anatomical responses to selective pressures in both lineages. As Janis & Fortelius (1988) noted, the evolution of hypsodonty — an increase in the height of the cusps of the teeth — is not a response to the pressure of increased wear that appears to be available to animals with bilophodont dentitions. The relatively few modifications of the molars that appear to have been possible in the animals under consideration were augmented by modifications of the supporting tissues to accentuate the food processing capabilities of the teeth while preserving relatively unworn tooth substance far into adult life. Selective feeding behaviour emerges as critical to the grazing adaptations of both groups, especially *T. gelada*, because of the lack of potential for generation of new tooth material once the adult ration has been exhausted.

In herbivorous mammals, the methods for mechanical breakdown of vegetation must complement those involved in chemical digestion, and both methods are clearly related to the metabolic rate of the animal under consideration. It is thus appropriate to consider how these parameters compare between the grazing macropodines and *Theropithecus*. As marsupials, grazing macropodines have lower metabolic rates than most placental mammals (McNab 1980). Their method of foregut fermentation permits them to break down the complex carbohydrates in cell walls, and their bilophodont molars serve the important function of chewing the food very finely in order to increase the surface area for microbial attack. Empirical determinations of basal metabolic rate in

geladas have not been performed, but evidence from the study of comparative brain volumes in cercopithecids suggests that their basal metabolic rate is low relative to closely related taxa of comparable body size (Martin 1993). Geladas are able to digest more than 50% of the crude fibre in their diet and appear to possess a hindgut microbial fauna for the fermentation of fibre (Iwamoto 1993b). Because of the limited capacity of geladas to digest the components of plant cell walls, their bilophodont molars must work to expose the contents of the cells by rupturing, as well as to finely comminute cell walls in preparation for microbial attack in the hindgut. Geladas are similar to ungulate hindgut fermenters in the ability to physically divide fibrous vegetation in the oral cavity, but they are less efficient at extracting protein (Dunbar & Bose 1991). In the dry season, when the nutritional value of grasses declines because of desiccation, geladas increase their grass intake, but supplement their diet with large volumes of the succulent herb *Trifolium* (Iwamoto 1993b). That geladas do not engage in the same degree of bulk feeding on grasses in the dry season as do ungulate hindgut fermenters reflects their limited ability to extract protein from this source.

When estimated metabolic requirements are taken into account, grazing macropodines and geladas appear to have similar compromises in their modes of physical and chemical breakdown of vegetation. The macropodines can satisfy their relatively low energy requirements and protein needs through the relatively slow and thorough chemical digestion of very finely divided grasses in the foregut. Geladas satisfy their higher energy requirements and protein needs by high-volume intake and fine physical reduction of consistently high-quality vegetation. This is followed by relatively fast "bulk processing" in the gut that involves only partial fermentation of ingesta in the hindgut.

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